

REVIEW: "A REVISION OF *HETEROTHECA* SECT. *PHYLLOTHECA* (NUTT.)
HARMS (COMPOSITAE: ASTEREAE)" BY J.C. SEMPLE

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ABSTRACT

A summary and overview are provided for the recent monograph of *Heterotheca* sect. *Phyllothea* by John Semple (1996), with emphasis on taxonomic concepts and implications of the formal taxonomic recognition of sympatric infraspecific taxa. Aspects of the taxonomy of sect. *Heterotheca* and sect. *Ammodia* also are discussed. Three new combinations allow a more evolutionarily congruent taxonomy for the *H. sessiliflora* complex: *H. sessiliflora* var. *thiniicola* (Rzed. & Ezc.) Nesom; *H. echioides* var. *bolanderioides* (Semple) Nesom; and *H. echioides* var. *bolanderi* (A. Gray) Nesom. Two combinations necessary in the same group remain to be formally completed by Semple. Rationale regarding the taxonomic status of *Bradburia* (independent genus vs. subgroup within *Chrysopsis*) is examined.

KEY WORDS: *Heterotheca*, *Bradburia*, *Chrysopsis*, Astereae, Asteraceae, nomenclature

John Semple (1996) has published "the first comprehensive monograph of the prairie and montane goldenasters, *Heterotheca* sect. *Phyllothea* (Nutt.) Harms." "This study was based on more than 10,300 herbarium specimens (6,844 separate collection numbers)" and includes specimen citations, typification, and a detailed illustration and distribution map for every taxonomic entity recognized in the treatment. An intuitive phylogenetic diagram (p. 6), drawn from molecular and morphological information, shows Semple's view of relationships among the goldenaster genera (subtribe Chrysopsidinae, sensu Nesom 1994) and provides a summary of the taxonomy and species relationships within sect. *Phyllothea*. There are taxonomic rearrangements, and two new species are described; one species is newly raised from varietal rank. The treatment also provides background for understanding nomenclatural combinations in sect. *Phyllothea* that were published earlier (Semple 1987, 1992, 1994). Most immediately, the value of the treatment is evident to anyone needing to identify plants of *Heterotheca*, but details of the nomenclature,

morphological accounts, and maps make it much simpler to comprehend the genus at all levels.

A synopsis of the history, morphology, and distribution of the goldenaster genera is presented at the beginning of the *Phyllotheca* monograph. The segregation of *Heterotheca*, *Chrysopsis*, and *Pityopsis* makes sense morphologically, cytologically, and phyletically, and those generic delimitations have gained increasing acceptance over the 20 years since publication of evidence for this system (Semple 1977; Semple et al. 1980). Among the goldenaster genera, *Heterotheca* is the largest and most taxonomically difficult. The complexity of the variation patterns apparently has long postponed a treatment of the largest part of the genus (sect. *Phyllotheca*), and in the wake of Semple's comprehensive study, it seems unlikely that anyone will be eager to begin any detailed process of reevaluation of the whole group.

An earlier review of Semple's treatise (Burk 1996, p. 219) speculated, however, that "because of its inherent variability, sect. *Phyllotheca* will continue to present difficulties for field biologists." The treatment will be subject to "the inevitable revisions of the 21st Century," and "if [Semple's taxonomic] structure is in time dismantled, he has nonetheless brought together here the building blocks to shape another." As with any study that pulls together such a large amount of information, unresolved problems also are brought to clearer focus, and the treatment provides an invaluable basis for further studies of the biology and evolution of these species. The present review provides an overview and perspective for some of the more interesting conclusions and questions that arise from the *Phyllotheca* monograph.

The 20 species (as recognized by Semple) of sect. *Phyllotheca* are a mixture of narrow endemics (e.g., *Heterotheca rutteri*, *H. marginata*, *H. jonesii*, *H. brandegeei*, *H. pumila*, *H. barbata*, *H. shevockii*, *H. monararchensis*, *H. mexicana*) and entities more widespread to varying degrees (e.g., *H. villosa*, *H. canescens*, *H. stenophylla*, *H. camporum*, *H. mucronata*, *H. zionensis*, *H. fulcrata*, *H. viscida*, *H. echioides*, *H. sessiliflora*). The most complex taxa are *H. villosa* (nine varieties, no subspecies) and *H. sessiliflora* (four subspecies, seven basic entities). *Heterotheca mucronata*, *H. camporum*, and *H. stenophylla* have two varieties each and *H. fulcrata* has four varieties.

Semple has dealt with the complex variation and difficulties in identification in a forthright way by separating specimen citations for collections that deviate from the typical form of the taxon. These are given in paragraphs (often several) after citations of "typical" collections with the heading of "aff. [the taxon under consideration]" followed by a parenthetical explanatory expression (e.g., "approaching var. *minor*" or "possible hybrids with *H. zionensis*"). A commentary on unusual variation for each taxon also is provided, and the indications of "aff." status are shown by distinct symbols on the distribution maps.

Taxonomic delimitations in sect. *Phyllotheca* are based in part on multivariate morphometric analyses "on more than 600 specimens including 76 type specimens," to be published separately (p. 2). Their publication will correspondingly contribute to an understanding of variation in sect. *Phyllotheca* and its taxonomic treatment. And "a cytogeographic study of the whole genus with a review of all previously published counts and new reports for several hundred individuals is in preparation" (p. 23).

Discussion of evolutionary processes underlying the variation patterns are found in the commentaries by Semple on individual species.

Among the most interesting features of the variation patterns described by Semple are the strongly overlapping geographic ranges in infraspecific taxa of most of the widespread species (especially see *H. sessiliflora*, *H. villosa*, *H. fulcrata*, and *H. mucronata*). Are these now sympatric entities recently spread from originally allopatric, more restricted ranges, with extensive hybridization resulting in blurred morphological boundaries in regions of overlap? Or, do these sympatric entities maintain their evolutionary independence to a significant degree? Evidence suggests that both situations may exist in sect. *Phyllotheca*.

"Within species, intervarietal hybrids are common in areas of sympatry" (p. 24), but these are usually between plants at the same ploidy level. Interspecific hybridization, however, is generally uncommon between diploids of sect. *Phyllotheca* but more common among tetraploids, suggesting that the difference in ploidy (between diploids and tetraploids) provides an effective isolating mechanism (see various comments below). Triploids are rarely encountered.

Taxonomic concepts

Indication of Semple's general approach toward fitting a nomenclatural system to the variation patterns is provided in commentary regarding *Heterotheca villosa*. "The races [= varieties, of *Heterotheca villosa*] fit well with the concept of variety in that each occurs in pure form in some populations, and the overall ranges are sympatric to a considerable degree with at least one other variety. Some taxa have sufficiently non-overlapping ranges that subspecies status might be considered. . . . Each variety most likely evolved in isolation and adapted to a different set of habitat parameters, but by and large no variety now occurs in isolation" (1996, p. 108). The biology and taxonomy of *H. villosa* and others (where the only infraspecific category is "var.") contrast in the *Phyllotheca* monograph with that of *H. sessiliflora* (where both "subsp." and "var." are used).

For a more detailed explanation of his concepts of subspecific and varietal categories, Semple refers to an earlier study of the genus *Xanthisma*: "A subspecies is characterized by all members exhibiting a particular morphology distinct from other individuals in the species and by the allopatric distribution of these members from the rest of the species" [citing various references] (Semple 1974, p. 4). "The variation between subspecies can be described as discontinuous, except for the few hybrids" (1974, p. 8). "A variety is characterized by all members of a population exhibiting a particular morphology distinct from other individuals in the species. The distribution of these populations is sympatric with populations whose members are not within the same variety, and also many populations of morphological intermediates exist [citing various references]. . . . Van Steenis described varietal level variation as being continuous with other varieties, although the continuum would have pronounced modes" (Semple 1974, p. 8-9).

Another perspective on Semple's varietal concept is found in his comments on *Heterotheca brandegeei*, which is markedly variable in glandularity and density of indument. The species is narrowly endemic to Sierra San Pedro Martir in Baja

California and is not suspected of intergrading with any other. "Even in a species with a limited distribution and a relatively few number of populations the full range in indument variation can be encountered. In other species with a greater range in [geographic] distribution than *H. brandegeei* (e.g., *H. sessiliflora*, *H. fulcrata*, *H. mucronata*, and *H. villosa*) past periods of isolation apparently have allowed fixation of different alleles controlling indument features in different portions of the range resulting in morphologically more well-defined races (generally labeled in this treatment as varieties)" (p. 66).

The taxonomic approach taken by Semple (recognition of numerous sympatric varieties) is perhaps by necessity a first step simply in providing a documented phenetic framework for the variation in this biologically complex group. Semple notes that this approach serves a related practical purpose. In discussing the strong similarity between *Heterotheca villosa* vars. *ballardii* and *foliosa* (both mostly tetraploid), he observes that if the diagnostic distinction of the former provides insufficient grounds for its formal recognition, "it then would be logical to merge all other varieties together with no infraspecific taxa being recognized in *H. villosa*. This would result in the loss from the formal nomenclature of a great deal of information on variation and distribution in what is admittedly a difficult species complex. Splitting seems justifiable in this case, and it maintains a nomenclature that parallels what has been adopted with less hesitation for other species in the section" (p. 114).

Still, if entities can be identified with some degree of consistency (as implied by the maps and specimen citations), and if they are sympatric and similar in habitat and phenology, some degree of internal reproductive isolation might be inferred to exist. Alternatively, segregation of linked genes controlling the character suites by which these taxa are identified may have a large effect on the variation patterns. Needed for interpretation, but missing in most cases, are observations on variation within populations of the taxa concerned. For those species where isolation does exist among the infraspecific taxa, the taxonomic approach could be shifted more toward an evolutionary perspective. Alternative taxonomic interpretations are possible, based on the same evidence and information.

Semple's approach to variation patterns and taxonomic applications in various species of *Heterotheca* is discussed below.

Heterotheca villosa/*stenophylla* var. *angustifolia*

Semple has transferred var. *angustifolia* of *Heterotheca villosa* to *H. stenophylla*. The latter species then becomes "divided into two seemingly quite distinct [and strongly sympatric] varieties that differ in gland and hair density" (p. 88). The transfer of var. *angustifolia* was made on the basis of "field experience and the results of multivariate analyses" showing that "the type of var. *angustifolia* is morphologically closer to many individuals of var. *stenophylla* than it is to either *H. canescens* or typical *H. villosa*" (p. 94).

Semple speculates that "tetraploid var. *angustifolia* originated from diploid var. *stenophylla* and subsequently converged toward tetraploid *H. canescens* due to putative occasional hybridization with the latter. . . . Alternatively, var. *angustifolia* might have originated via allopolyploidy from more hairy and less glandular diploid *H.*

stenophylla var. *stenophylla* and *H. canescens*" (p. 94). *Heterotheca stenophylla* and *H. canescens* are shown as sister species in Semple's phylogram.

Based on Semple's estimate of its evolutionary origin, var. *angustifolia* could justifiably be treated within or close to either of the two contributors to its genome: (a) *Heterotheca stenophylla* and (b) *H. canescens*.

(a) "The range of var. *angustifolia* is generally the same as that of var. *stenophylla* from Oklahoma northward, except that var. *angustifolia* occurs over a slightly greater area and in the gaps between the disjunct populations of var. *stenophylla*" (p. 94). "The two varieties occur in pure and mixed populations throughout the range of the species" (p. 53). Cytological evidence seems unequivocal in suggesting that var. *angustifolia* is genetically isolated from var. *stenophylla*. Most chromosome number reports for var. *stenophylla* have been of diploids, while all of many reports for var. *angustifolia* have been of tetraploids. "Several triploid counts [have been reported] from putative intervarietal hybrids" (p. 92).

(b) *Heterotheca canescens* also is mostly diploid over its range and also is broadly sympatric with var. *angustifolia*. The only intermediate collections cited by Semple for *H. canescens* are those "aff. *H. canescens* (close to *H. stenophylla* var. *angustifolia*)" (p. 100). Presumably, var. *angustifolia* - *H. canescens* hybrids are triploid.

Because var. *angustifolia* is broadly sympatric with both of its putative parents and apparently genetically isolated from them to a significant degree, its treatment at specific rank also is a possibility. It presumably is an evolutionarily distinct entity and its morphogeographic circumscription is the same regardless of its taxonomic placement.

If Semple's hypothesis of origin for var. *angustifolia* is correct, placement of it within *Heterotheca stenophylla* is better than within *H. villosa*. Inclusion of var. *angustifolia*, however, only slightly increases the morphological complexity of *H. villosa*, as defined by Semple, and occupies a part of the overall geographic range where its sympatry with conspecific varieties is relatively less (Figs. 39 and 40).

Heterotheca villosa

Heterotheca villosa is "highly variable in diagnostic features" and is "difficult to define as a species, although each infraspecific taxon has a diagnostic suite of traits." The species is "very variable in stem height, leaf base shape, stem and leaf indument traits, numbers of heads per capitulescence and florets per head" (p. 105). It is "defined by what it lacks rather than what it possesses" (p. 108).

Nine varieties are recognized within *Heterotheca villosa* in 1996, but Semple's concepts of these taxa have fluctuated. In 1990, he placed a number of names as synonyms of *H. villosa* var. *hispida* (= *H. villosa* var. *minor* of 1996) with the following comment: "Included are morphotypes that I have previously accepted as species or subspecies (Semple 1987), but have come to view as sometimes semi-distinct regional 'races' that grade into each other to such an extent that continued recognition cannot be justified with the data available to me at present." Later (1994, 1996), apparently based on multivariate studies, he returned to his earlier position of

formally recognizing these races, including four varieties within *H. villosa* from the same 1990 list of synonyms. "A number of morphotypes [of *H. villosa*] appear sufficiently distinct to warrant recognition. . . . All races have well defined geographic distributions which overlap to a considerable degree in some cases (Figs. 39-40). The highly plastic nature of the species and undoubted hybridization make identification to variety difficult in numerous cases" (1996, p. 108).

"The diploid races [of *Heterotheca villosa*] are usually distinct from each other, but each has given rise to one (or more) tetraploid lines [exception noted below]. Tetraploids ['more common than diploids in *H. villosa*'] tend to look more alike because the diploid traits are less pronounced and because the tetraploids are more likely to have hybridized, thus further blurring the distinctions between the races. Possible occasional hybridization with tetraploids in other species may also have further buffered the distinctive morphology of the tetraploid level of the pillar complex" (p. 108).

Some infraspecific taxa of *Heterotheca villosa* are more distinct than others. Two have been regarded as species in recent floristic treatments: (a) var. *nana* (as *H. horrida*, e.g., Correll & Johnston 1970; Dorn 1988) and (b) var. *depressa* (as *H. depressa*, Dorn 1988). The distinctiveness of these entities is further emphasized by the relatively few collections cited for them as "aff." Treatment of var. *nana* and var. *depressa* at species rank appears to be a reasonable alternative potentially providing a closer match between taxonomy and the evolutionary pattern.

(a) Var. *nana* (diploid, many counts, without tetraploid populations) is almost completely overlaid in its geographic range by var. *foliosa* (diploid and tetraploid but tetraploid in its area of overlap with var. *nana*, many reports) and by var. *minor* (diploid and tetraploid, numerous reports). Intermediates between var. *nana* and var. *scabra* occur in the Four Corners area; the closest relative of var. *nana* is the narrow endemic var. *sierrablancensis* (diploid), which occurs at the southeastern corner of the range of var. *nana*.

(b) Var. *depressa* (tetraploid, several counts, with only a speculative evolutionary connection to diploids) is endemic to habitats connected with hot springs and geyser basins mostly in the area of Yellowstone National Park. Putative hybrids have been observed between var. *depressa* and var. *minor*, which is sympatric but different in habitat.

Heterotheca villosa var. *pedunculata* also has distinctions that set it apart from other taxa within *H. villosa*. "Semple (1990) included it among tentative synonyms of var. *villosa*, but the results of multivariate analyses conducted since then indicate that it is sufficiently distinct from var. *villosa* to warrant recognition even when only non-diagnostic traits are used in the discriminant analysis. It is the only usually tetraploid taxon in sect. *Phyllotheca* that has very densely pubescent leaves" (1996, p. 124). Intergrades occur between var. *pedunculata* and var. *minor* (tetraploid) and var. *scabra* (tetraploid).

Var. *pedunculata* "is similar to the recently described *Heterotheca mexicana*, which has achenes with a weakly developed short outer pappus whorl. If the more pubescent forms of the Mexicana complex [*H. mucronata*, *H. gypsophila*, *H. mexicana*] are primitive in the section, then var. *pedunculata* is likely to be similar to the ancestral

form of *H. villosa* from which other taxa evolved . . ." (1996, p. 124). These comments seem to imply that var. *pedunculata* is closely related to the Mexicana species, but there apparently is no further development of the hint that the Mexicana complex may be primitive within sect. *Phyllothea*. Nor does the 1996 phylogram support this point of view. The phylogram also places *H. villosa* in a position widely separated from the Mexicana complex.

Heterotheca mucronata

Semple has described *Heterotheca mucronata* var. *harmsiana* (var. nov.) from the northeast Mexican states of Tamaulipas, Nuevo León, San Luis Potosí, and Coahuila. Var. *harmsiana* differs from the typical variety in its leaves with "fewer hairs and more glands," illustrating Semple's observation (p. 94) that "most other species [of sect. *Phyllothea*] include both more glandular and more hairy races." Var. *mucronata* and var. *harmsiana* have essentially congruent geographic distributions and both have been collected from at least six of the same localities or localized areas from a relatively small region within Nuevo León and Coahuila (see specimen citations for the two taxa): the Peña Nevada area; east of Iturbide; Chipinque; Sierra de la Viga; Sierra de Arteaga; and Cañon de San Lorenzo.

My own field and herbarium experience have indicated that only a single evolutionary entity exists among plants identified as *Heterotheca mucronata*. Plants from Tamaulipas and near Linares in southeastern Nuevo León have eglandular leaves and a more densely sericeous vestiture of thinner-based trichomes than those in the remainder of the Mexican range of the species (pers. observ.), but the distribution of these variants does not match the distribution of var. *mucronata* described by Semple. Putative intergrades with *H. fulcrata* (see below) have been collected around Saltillo, Coahuila, and slightly to the south in northern Zacatecas.

The recognition within *Heterotheca mucronata* of closely sympatric varieties with no apparent difference in habitat or phenology suggests that the taxa recognized are inter- or infra-populational variants differing in the expression of two types of trichomes. Local adaptation and genetic segregation could account for differentiation among and within populations. An independent evaluation would be useful to resolve the differences in perception of these variation patterns, but differences in our concepts of the varietal category apparently preclude any chance of taxonomic agreement.

Heterotheca fulcrata

The distinctive species *Heterotheca fulcrata* comprises four varieties in Semple's concept. Numerous reports of diploid chromosome numbers have been reported for all of them (plus one "unconfirmed" tetraploid count for var. *fulcrata*). Vars. *fulcrata*, *arizonica*, and *senilis* are sympatric with nearly congruent ranges in the montane habitats of the Chihuahuan Desert region in northeastern México and trans-Pecos Texas and from there into southern New Mexico and Arizona. I have identified these plants in México as a single evolutionary entity (= *H. fulcrata*). The overall geographic distributions of var. *fulcrata* and var. *amplifolia* (sensu Semple) also are remarkably similar, as are those of var. *arizonica* and var. *senilis*. In fact, given the apparent cohesiveness of the species, evidence suggests that the varieties (sensu

Semple) of *H. fulcrata* are better regarded as local variants in the sense of most current botanists, perhaps treated with taxonomic status as "forma," which would retain the formal nomenclature desired for these entities by Semple (see "Taxonomic Concepts," above).

Heterotheca sessiliflora complex

Within the primarily Californian *Heterotheca sessiliflora* complex, Semple has fashioned an amalgum of greatly increased complexity by combining *H. echioides*, *H. camphorata*, *H. bolanderi*, *H. fastigiata*, and *H. sessiliflora* into a single species (*H. sessiliflora*). Four of these are treated at subspecific rank (subsp. *echioides*, *bolanderi*, *fastigiata*, and *sessiliflora*); *H. camphorata* is treated as a variety and placed within subsp. *echioides*. Varieties are recognized within subsp. *fastigiata* (2 vars.) and subsp. *echioides* (3 vars.); subsp. *sessiliflora* and *bolanderi* are monotypic. *Heterotheca monarchensis* is a narrow endemic from the Kings River canyon in Fresno County. It is similar to *H. echioides* but is morphologically distinct and geographically separated from other members of the *H. sessiliflora* complex.

Semple's Figure 14 maps the geographic distribution of the basic taxa of *Heterotheca sessiliflora* as he has defined that species. Four varieties of *H. sessiliflora* are sympatrically overlaid in Los Angeles County, three each in San Bernardino and Ventura counties. Var. *camphorata* is closely sympatric with var. *echioides* in Monterey, Santa Clara, and Santa Cruz counties.

Without disagreement regarding delimitation of the basic evolutionary units of the *Heterotheca sessiliflora* complex, they can be positioned in a way that more closely matches the evolutionary situation by essentially eliminating sympatric entities within a single species. A taxonomic arrangement to accomplish this is suggested below (Fig. 1), contrasted with Semple's arrangement of the same basic entities (Fig. 2). Continuing elimination of natural habitats and creation of hybrid habitats by human activities might drive this whole complex toward a genetic swarm, but the suggested alternate arrangement preserves the morphological coherence of the taxa involved and provides a more comprehensible tool for dealing with the current morpho-geographic pattern of variation. Based on the information presented by Semple, and in my experience, the *H. sessiliflora* complex (sensu Semple) is significantly different from most other *Heterotheca* species of this treatment that are divided into sympatric varieties.

Semple's basic units in the *Heterotheca sessiliflora* complex are a mix of subspecies and varieties. He did not treat the entities subsp. *sessiliflora* and subsp. *bolanderi* at varietal rank, apparently because both are restricted to coastal strand habitats and neither is geographically overlapping with any other taxa (see definitions above of variety and subspecies). Formal varietal combinations were not provided for "var." *fastigiata* and "var." *echioides*, although it appears that this was intended, as they are repeatedly referred to as "var. *fastigiata*" and "var. *echioides*" and shown on the phylogram as entities coordinate with other varieties. The count of "24 varieties" in the Abstract also must include "var. *fastigiata*" and "var. *echioides*."

Heterotheca sessiliflora (Nutt.) Shinnery
 var. *sessiliflora*
 var. *fastigiata* (Greene) Semple, ined. [nom. nud. in Semple 1996]
 var. *sanjacintensis* Semple
 var. *thiniicola* (Rzed. & Ezc.) Nesom

Heterotheca echioides (Benth.) Shinnery
 var. *echioides*
 var. *bolanderioides* (Semple) Nesom
 var. *bolanderi* (A. Gray) Nesom

Heterotheca camphorata (Eastw.) Semple

Heterotheca monarchensis York, Shevock, & Semple

Figure 1. Alternate taxonomy for the *Heterotheca sessiliflora* complex. Except for var. *fastigiata*, nomenclatural combinations to formally complete this are provided below.

Heterotheca sessiliflora (Nutt.) Shinnery
 subsp. *sessiliflora*
 subsp. *fastigiata* (Greene) Semple
 var. *fastigiata* (Greene) Semple, ined. [nom. nud. in Semple 1996]
 var. *sanjacintensis* Semple
 subsp. *echioides* (Benth.) Semple
 var. *echioides* (Benth.) Semple, ined. [nom. nud. in Semple 1996]
 var. *bolanderioides* Semple
 var. *camphorata* (Eastw.) Semple
 subsp. *bolanderi* (A. Gray) Semple

Heterotheca thiniicola (Rzed. & Ezc.) B.L. Turner

Heterotheca monarchensis York, Shevock, & Semple

Figure 2. Semple's taxonomy for the *Heterotheca sessiliflora* complex. See comments in text regarding "ined." nomenclature.

The alternate arrangement adopts Semple's suggestions in combining *Heterotheca fastigiata* with *H. sessiliflora* and *H. bolanderi* with *H. echioides*, adding a newly described variety to each species. *Heterotheca bolanderi* (diploid) is discrete in geography and habitat and might be kept as a distinct species, but it is closely similar to var. *echioides* and var. *bolanderioides* and may have been directly involved in the parentage of the latter, which is primarily tetraploid (fide Semple, p. 49). *Heterotheca camphorata* (mostly diploid) is kept as a separate species (with a combination made earlier by Semple) and *H. thiniicola* is brought within *H. sessiliflora* (comments below). This arrangement does not eliminate difficulties in identifying hybrids, introgressants, and other intermediates for whatever reason, but such problems exist no matter what taxonomic superstructure is laid over the basic evolutionary units. The most common interspecific hybrids in the suggested alternate arrangement appear to be between *H. echioides* (var. *echioides*) and *H. sessiliflora* (var. *fastigiata*) where they are sympatric in San Bernardino, Los Angeles, and Ventura counties.

Heterotheca sessiliflora (s. str.), like *H. bolanderi*, is a coastal strand entity discrete in geography and habitat, but Semple's proposal to unite it with *H. fastigiata* is a good one. The four varieties of *H. sessiliflora* (as suggested here) are exclusively diploid and distributed allopatrically in southwestern California and northwestern México (Baja California and Sonora). A sericeous indument of short hairs and leaves with distinctly wavy margins unite this group of plants and give it an immediately recognizable appearance.

In a treatment of Mexican *Heterotheca* (Nesom unpublished), *H. thiniicola* (a desert habitat population from northwestern Sonora) has been included in the same circumscription as the type of *H. fastigiata*. Semple, in contrast, has maintained *H. thiniicola* at specific rank, noting (p. 54) that "While similar to var. *fastigiata*, *H. thiniicola* is sufficiently different to warrant recognition as a separate taxon. Its unique habitat indicates that it is more than just a disjunct population of the montane var. *fastigiata*."

The only differences I can confirm to separate *Heterotheca thiniicola* from *H. sessiliflora* var. *fastigiata* are those noted by Semple: the absence of osteiform (Type A) trichomes on the disc corollas of the former, its distinctly desertic habitat at 110 meters elevation, and a geographic disjunction of about 200 miles from other *H. sessiliflora*. Var. *fastigiata*, however, occurs in habitats at "(150) -300-1800- (2200)" meters elevation, low enough to include "desert washes," although its primary habitat is higher in "pine forests and transition chaparral" (p. 40). Semple has made the useful observation that the consistent occurrence of osteiform trichomes on the disc corollas is evidence for monophyly of the *H. sessiliflora* complex (sensu Semple, including *H. monarchensis*) --- the absence of these trichomes on *H. thiniicola* corollas almost certainly has resulted from a recent evolutionary loss (vs. primitive absence) and does not suggest the species should be considered apart from var. *fastigiata*, to which it is otherwise nearly identical. To formally recognize the evolutionary independence (via geographic isolation) of the Sonoran population and its small degree of morphological divergence, it is treated here at varietal rank within *H. sessiliflora*, coordinate with the other three varieties.

Heterotheca sessiliflora (Nutt.) Shinners var. *thiniicola* (Rzed. & Ezc.) Nesom, *comb. nov.* BASIONYM: *Haplopappus thiniicola* Rzed. & Ezc., *Cienc. Interamer.* 26:16. 1986. *Heterotheca thiniicola* (Rzed. & Ezc.) B.L. Turner, *Phytologia* 63:128. 1987.

Heterotheca echioides (Benth.) Shinners var. *bolanderioides* (Semple) Nesom, *comb. nov.* BASIONYM: *Heterotheca sessiliflora* (Nutt.) Shinners var. *bolanderioides* Semple, *Phytologia* 73:450. 1992.

Heterotheca echioides (Benth.) Shinners var. *bolanderi* (A. Gray) Nesom, *comb. nov.* BASIONYM: *Chrysopsis bolanderi* A. Gray, *Proc. Amer. Acad. Arts* 6:543. 1866. *Heterotheca bolanderi* (A. Gray) Harms, *Brittonia* 26:61. 1974.

Species concepts in sect. *Heterotheca*

Semple recognizes seven species of sect. *Heterotheca* (see p. 25: "Key to *Heterotheca* sect. *Heterotheca* [after Wagenknecht, 1960, with modifications]"), noting that my approach (Nesom 1990) contrasted with that of Wagenknecht. He adopted Wagenknecht's definitions of taxa without commenting on the suggestion that *H. subaxillaris* be broadened to include *H. latifolia* (including varieties), *H. psammophila*, and *H. chrysopsidis*. Regional morphological tendencies in *H. subaxillaris* can be recognized, but my brief study was unsuccessful in sorting out morpho-geographic "nodes" in this phenotypically malleable complex that could be unarbitrarily recognized. Nor has anyone provided a documented (specimen-based) map showing the distribution of these taxa. Commenting on previous studies of sect. *Heterotheca*, including Wagenknecht's, Harms (1968, p. 9) observed that "Perhaps this entire [*H. subaxillaris*] complex should still be accepted as a single, polymorphic, polytypic species." Lammers (1997), in contrast, apparently has identified *H. latifolia* (as distinct from *H. subaxillaris*) with confidence and is able to distinguish all three varieties of *H. latifolia*.

Semple's key to sect. *Heterotheca* gives an overview of the typological concepts in the *H. subaxillaris* complex that may be applied to indicate that one or another plant approaches the typical morphology of a named taxon, but either extensive interregional gene flow or weak primary differentiation, or both (see comments by Burk 1961, 1966), have not made it simple to find geographic patterns to which a meaningful (predictive) taxonomy can be applied. Field and lab study may yet show that such patterns and evolutionary entities exist, but as indicated earlier (Nesom 1990), it will be a considerable challenge to provide this evidence.

Taxonomy of *Heterotheca* sect. *Ammodia*

A taxonomic study of the single species of sect. *Ammodia* (*Heterotheca oregona*) was published earlier (Semple *et al.* 1988). The treatment of infraspecific variation there is similar to that in sect. *Phyllothea*. Four partially sympatric entities with "no

indication of any pronounced differences in habitat preference" (p. 554) were found to separate with little or no overlap in a multivariate analysis. Following earlier criteria (e.g., Semple 1974), "varietal rank was determined to be most appropriate. The ranges of the four races overlap to a great extent in California, which precludes subspecies status, although each has a unique range" (1988, pp. 549-550). Chromosome numbers have been reported for three of the varieties: all are diploid.

"The varietal differences [within *Heterotheca oregona*] are thought to have evolved as a consequence of geographic isolation. During the Holocene, migration and range expansions have eliminated the spatial isolation and the sympatric races now hybridize" (1988, p. 553). Non-overlap in multivariate analyses, however, and a low frequency of intermediacy ("about 10% of all herbarium specimens . . . studied") seem to indicate that the infraspecific taxa may be separated by substantial internal reproductive isolation. As presented by Semple *et al.* (1988), information suggests that these closely sympatric but little intergrading entities with small morphological differences may be biological microspecies.

Status of *Bradburia*

Semple notes that "circumscription of all the generic limits of the goldenasters remains in turmoil" (p. 7). His only example, however, of problematic generic limits is the question of taxonomic rank for *Bradburia* (as a separate genus vs. a subgroup within *Chrysopsis*). Turmoil is not evident, and given increasing agreement with Semple's arrangement of *Heterotheca*, *Chrysopsis*, and *Pityopsis*, the only controversy appears to involve the *Bradburia* question and what it may imply (for consistency) about the relationship of sect. *Heterotheca* to the rest of the genus (*sensu* Semple).

In contrast to my decision to merge the genus *Bradburia* with *Chrysopsis* as sect. *Bradburia* (enlarged to two species with the addition of *Chrysopsis pilosa*, Nesom 1991a), Semple has decided to retain *Bradburia* as a separate genus including the same two species. He has observed the close similarity and relationship between *B. hirtella* and *C. pilosa* (Semple & Chinnappa 1984) and accepts the results of recent morphological analyses (Nesom 1991a) and molecular analyses (Lane *et al.* 1996) that place them as sister species. These two, in turn, are the sister group to the rest of *Chrysopsis* in phyletic analyses including other taxa of goldenasters (Nesom 1991b; Lane *et al.* 1996) as well as in Semple's own diagram of goldenaster relationships (1996, p. 6).

Semple's published justification for maintaining *Bradburia* at generic rank is solely his view that a ditypic *Bradburia* could serve as an "alternative solution to the generic limits problem surrounding the goldenasters" (p. 7). He has neither indicated on what grounds he prefers one alternative rather than the other nor provided any discussion of the relative merits or problems regarding the choice of options. Based on his comments and distribution maps, the distinctions between the two genera are summarized as follows.

1. Perennial; leaves and stems with "distinctly flagelliform hairs"; cells of disc corolla throat with elongate crystals; Florida to Mississippi, Louisiana, and Texas, but mostly east of the Mississippi River. *Chrysopsis*

1. Annual or perennial; leaves and stems with "less to non-flagelliform hairs"; cells of disc corolla throat without crystals or crystals reduced in size; Texas and Louisiana to Missouri and Kansas, Tennessee, Mississippi, and Alabama, but mostly west of the Mississippi River. *Bradburia*

Additionally (Nesom 1991a), these two species differ as a pair from other *Chrysopsis* in longer flowering branches, scarious-margined phyllaries, sharp-pointed sweeping hairs on the style branches, and karyotype.

If the characterization of *Bradburia hirtella* and *Chrysopsis pilosa* as sister species is correct, and if these two are phylogenetically coordinate with the rest of *Chrysopsis*, taxonomic treatment of a ditypic *Bradburia* at either rank (within or distinct from *Chrysopsis*) is consistent with the phylogeny. My study also noted that the enlargement of an independent *Bradburia* was an alternative solution (Nesom 1991a, p. 111): "*Chrysopsis pilosa* and *Bradburia* are so distinct as a pair that *C. pilosa* might justifiably be transferred to *Bradburia*." Does available evidence support a decision regarding the taxonomic placement of ditypic *Bradburia*? And which treatment is more consistent with existing taxonomic arrangements within the Chrysopsidinae?

Within the goldenaster group (subtribe Chrysopsidinae), ditypic *Bradburia* is united with *Chrysopsis* (sensu Semple) by a set of cytological and morphological features: reduced base chromosome number ($x=5$ or 4; shared with the genus *Osbertia*); long, smooth-walled osteiform trichomes often conspicuously drawn out into flexuous, filamentous extensions; achene shape obovate and asymmetric (shared with sect. *Heterotheca*); achene surfaces with thick, rounded ridges, the nerves completely below the epidermal surface; and pappus insertion inset from the shoulder rim of the achene apex. A significant degree of genetic similarity between the two segments of *Chrysopsis* was demonstrated by hybrids between *C. pilosa* (sect. *Bradburia*) and *C. gossypina* (sect. *Chrysopsis*) synthesized by Semple (1981), who then viewed *C. pilosa* as the sister species to *C. gossypina* and justifiably treated within *Chrysopsis*. As noted above, molecular data also indicates that *Bradburia/Chrysopsis* is monophyletic.

The relationship of ditypic sect. *Bradburia* to the rest of *Chrysopsis* appears to be analogous to the relationship of sect. *Heterotheca*, and perhaps of sect. *Ammodia*, to the rest of the genus *Heterotheca* (sect. *Phyllothea*). Semple (1996) considers sect. *Heterotheca* to be the sister group to rest of the genus, sect. *Ammodia* phylogenetically coordinate with sect. *Heterotheca*. My cladistic analysis (Nesom 1991b) placed sect. *Ammodia* basal within the genus and sect. *Heterotheca* among other clades, but only weak characters supported this. Sect. *Heterotheca* is a distinct and clearly monophyletic group, but Harms (1965) synthesized viable hybrids between *H. subaxillaris* (sect. *Heterotheca*) and *H. canescens* (sect. *Phyllothea*). The option ("alternative solution") of segregating sect. *Heterotheca* as a small genus within the goldenasters has often been followed, with the remainder of the *Heterotheca* species placed into an expanded *Chrysopsis*. If sect. *Heterotheca* were segregated today, however, the generally accepted redefinition of *Chrysopsis* would necessitate recognition of a new genus to accommodate the species of sects. *Phyllothea* and *Ammodia*. Nevertheless, Semple's rationale for segregating *Bradburia* as a genus

provides a similar one for the treatment of *Heterotheca* s. str. The monotypic sect. *Ammodia* also has been treated as a separate genus (Nuttall 1841) and could be again.

Available evidence and the current taxonomy of the Chrysopsidinae indicate to me that ditypic *Bradburia* (in the current view of its phylogeny) is better viewed as a well-defined subgroup of *Chrysopsis* rather than a weakly separated genus.

ACKNOWLEDGMENTS

I am grateful to John Strother, John Kartesz, and Billie Turner for their comments on the manuscript.

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